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The labyrinthine morphology of *Pronycticebus gaudryi* (Primates, Adapiformes)

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Abstract

The publication of a well preserved Eocene primate, *Darwinius masillae* (Cercamoniinae, Notharctidae), has revived the debate on the phylogenetic relationships of Adapiformes and extant primates (Franzen et al. 2009). Recently, Lebrun et al. (2010) showed that the morphology of the bony labyrinth of strepsirrhine primates conveys a strong phylogenetic signal. The study of labyrinthine morphology may thus bring a new piece of evidence to resolve phylogenetic relationships within a group. The investigation of the labyrinthine morphology of another Cercamoniinae, *Pronycticebus gaudryi*, reveals no synapomorphy with the labyrinths of modern anthropoids. On the contrary, *Pronycticebus* is closer in labyrinthine shape to extant strepsirrhines, which supports the hypothesis that the Cercamoniinae and other Adapiformes are the sister group of toothcombed primates.

Keywords : Adapiformes; geometric morphometrics; inner ear; primates; strepsirrhini.

Introduction

The recent description of *Darwinius masillae* (Cercamoniinae, Notharctidae), a well preserved Eocene primate, has revived the debate on the phylogenetic relationships of Adapiformes and anthropoid primates (Franzen et al. 2009). Several decades ago, a few researchers had argued that extant anthropoids share an adapiform ancestor (Franzen 1994; Gingerich 1973, 1975, 1981; Gingerich and Schoeninger 1977; Rasmussen 1986, 1990). Since then, phylogenetic analyses of primate relationships have favored the hypothesis that Adapiformes are stem strepsirrhines (see for instance Kay et al. 1997; Marivaux et al. 2005; Ni et al. 2004;

Ross et al. 1998; Seiffert et al. 2005). However, Franzen et al. (2009) have revived the hypothesis of a special link between Adapiformes and anthropoids, claiming that *Darwinius masillae* was part of a group “representative of the early haplorhine diversification”. This view was criticized by Williams et al. (2010), in a review of the anatomical features differentiating haplorhine and strepsirrhine primates. Williams et al. (2010) argued that *Darwinius* is certainly not a haplorhine, and gave further support to the hypothesis that Adapiformes are basal strepsirrhines (but see Gingerich et al. 2010).

In this paper, we analyse the phylogenetic relationships of Adapiformes with other primates from the perspective of the morphology of the inner ear. Morphological variation of the bony labyrinth across taxa reflects differences in locomotor behavior (Silcox et al. 2009; Spoor and Zonneveld 1998; Spoor et al. 2007; Walker et al. 2008) and hearing performance (Coleman and Boyer 2012; Coleman and Colbert 2010; Coleman et al. 2010; Echterler et al. 1994; Gleich et al. 2005; Kirk and Gosselin-Ildari 2009; West 1985). This structure is thus highly functionally constrained. Nevertheless, a part of labyrinthine morphological variation may still convey phylogenetic information. Basilar membrane length, the number of spiral turns and cochlear volume relate to low frequency and high frequency sensitivity (Coleman and Boyer 2012; Echterler et al. 1994; Kirk and Gosselin-Ildari 2009; West 1985). However, other aspects of the morphology of the cochlea, such as its general geometry and orientation relative to the semi-circular canal system are less likely to reflect hearing performance. Concerning the semi-circular canal system, even though canal radius tends to increase with agility, semi-circular canal morphology conveys a strong phylogenetic signal (Spoor et al. 2007). As large species tend to be less agile than small ones, a possible way to maximise the phylogenetic information conveyed by this structure is to remove the allometric component of labyrinthine morphological variation.

Building on these hypotheses, Lebrun et al. (2010) proposed a protocol analysis designed to capture the allometry-free component of the geometry of the semi-circular canal system, and the general orientation and geometry of the cochlea within the labyrinth. These authors showed that in strepsirrhine primates the geometry of the bony labyrinth conveys a strong phylogenetic signal. Also, they showed that change in labyrinthine morphology is adequately described with an evolutionary random walk model, i.e. random phenotypic dispersal in morphospace.

Under this hypothesis, average shapes calculated for each node of a phylogenetic tree give an estimate of the inner ear morphology of the respective last common ancestors (LCAs). Lebrun et al. (2010) showed that the morphology of Eocene Adapinae is close to the inferred state of the ancestral toothcombed primate labyrinthine morphology. Besides, adapine labyrinthine morphology is close to that of Malagasy primates, which supports the hypothesis that Adapiformes are the sister group of toothcombed primates.

The morphology of the inner ear of *Darwinius masillae* is not preserved (Hurum 2011). However, a more complete and undistorted cranium of another member of Cercamoniinae, *Pronycticebus gaudryi*, is available for study. The ear region of *Pronycticebus* is well preserved. The bullae were intact when the specimen was discovered (Grandidier 1904), and were subsequently partially prepared. A small segment of a free ectotympanic ring was exposed and described by Simons (1962) as *Loris*-like. Other students rather described the ear region of *Pronycticebus* as *Lemur*-like, a free floating ectotympanic ring being actually found in Malagasy primates (Couette et al. 2011; Le Gros Clark 1934; Saban 1963; Szalay 1971), giving support to the strepsirrhine status of *Pronycticebus*. Because the bullae of the type specimen are filled with a hard calcitic matrix, the specimen was never completely dissected. However, CT scan techniques allow for virtual and non-invasive dissection of the that region. Investigation of the morphology of the labyrinth of *Pronycticebus* was done, and study of its morphological affinities with that of extant primates and other Eocene primate taxa shall provide an independent piece of evidence to test hypotheses about the phylogenetic relationships of Adapiformes with other primates (Lebrun et al. 2011). Our earlier analyses showed that primate labyrinthine morphology is consistent at the family level, and exhibits an even higher degree of consistency at the subfamily level (Lebrun et al. 2010). Building upon these findings, we make the assumption that the labyrinths of *Darwinius masillae* and of *Pronycticebus gaudryi* share strong morphological affinities. Also, the teeth of *Darwinius* show derived similarities with those of *Agerinia* (Herbomel and Godinot 2011), and *Agerinia* and *Pronycticebus* have been considered as closely related (Godinot 1998; Szalay 1971). Hence *Darwinius* is probably quite closely related with *Pronycticebus gaudryi*, and the labyrinth of the latter is likely a good proxy for that of *Darwinius masillae*.

Materials and Methods

Comparative sample

We compare the labyrinth of *Pronycticebus* with a broad sample of extant and extinct primates, in order to have a good representation of present and past primate labyrinthine morphological diversity. The comparative dataset consists of 93 inner ears of primates (see Table 1). Thirty-nine inner ears belong to modern strepsirrhine taxa, representing 14 lemuroid and 9 lorisoid genera. Forty-two modern haplorhine specimens were digitized, representing 16 genera of platyrrhines, 20 genera of catarrhines and the genus *Tarsius*. Concerning the fossil sample, 11 inner ears of Adapiformes were included, representing 3 adapine genera and the cercamoniine *Pronycticebus*. Finally, 2 inner ears of fossil Omomyiformes belonging to the Microchoerinae subfamily were analysed (see Table 1). Only left inner ears were integrated in the sample when preserved. For the four adapine specimens which had only their right inner ear preserved, virtual mirror images of their right labyrinth were produced and used for analysis.

Data acquisition

X-ray micro-computed tomography (μ CT) and synchrotron X-ray microtomography (SR- μ CT) were used to acquire 3D data. Most fossil specimens were scanned at the European Synchrotron Radiation Facility (ESRF) on beam lines ID17 and ID19 (see Table 1). Synchrotron tomography results in high contrast and spatial resolutions data (Tafforeau et al. 2006), which greatly facilitate segmentation of the bony labyrinth cavities filled by dense sediment when fossils are highly mineralized (Lebrun et al. 2010). Digital volume data of *Pronycticebus gaudryi* were obtained via high resolution micro-CT on a SkyScan 1076 scanner. Three-dimensional surfaces representing the bony labyrinths were produced with Amira 3.1.1 (Visage Imaging) and Avizo 6.3.1 (Visualization Sciences Group) via thresholding using the half maximum height technique (Spoor et al. 1993) and manual segmentation. The choice of the threshold value could affect to some extent the reconstruction of the semicircular canals and of the cochlea (Coleman and Colbert 2007). Fortunately, thresholding effects do not affect the location of the lumen centre of the semicircular canals and the cochlea (Gunz et al. 2012; Lebrun et al. 2010). As such, labyrinthine shape was quantified with 22 landmarks, located

at the centres of the lumina of the semicircular canals, of the ampullae, and of the cochlear helix (see Supporting Information Figure S1), following the protocol of Lebrun et al. (2010).

Data analysis

Using generalized least-squares fitting (Rohlf, 1990) and principal components analysis (PCA) of shape (Dryden & Mardia, 1998), the form of each specimen's landmark configuration was represented by its centroid size S , and by its multidimensional shape vector v in linearized Procrustes shape space. In order to take into account potential confounding effects of size allometry on primate labyrinthine shape (Lebrun et al. 2010), size-corrected shapes were obtained as follows. Regression of Procrustes coordinates by the logarithm of centroid size were computed for Lorisoidea, Lemuroidea, Catarrhines, Platyrrhines, Adapiformes, Omomyiformes, and Tarsiiformes, yielding group-specific allometric shape vectors (ASV_g). The ASV_g represent directions in shape space which characterize group-specific allometric patterns of labyrinthine shape variation. A common allometric shape vector (ASV_c), obtained as the mean of all the ASV_g , provided a direction in shape space that minimizes potential divergence in labyrinthine allometric patterns across taxonomic groups. All labyrinths were then projected on ASV_c , the residuals representing the size-independent component of labyrinthine shape. Size-independent shape variation was analyzed by principal components analysis (PCA) of shape using the interactive software package MORPHOTOOLS (Lebrun 2008; Specht 2007; Specht et al. 2007).

In order to assess the morphological affinities of *Pronycticebus* with extant primates, Adapinae and Microchoerinae, phenetic trees were produced as follows. For each group (Adapinae, Microchoerinae, Lemuroidea, Lorisoidea, *Tarsius*, Catarrhines, Platyrrhines), an average size-corrected labyrinthine shape was produced. Taxa were then clustered using the NJ (neighbour joining) procedure. A landmark-based random sampling procedure, as described in Lockwood et al. (2004), was executed 1000 times. The associated consensus NJ tree was computed using PHYLIP (Felsenstein 1989).

Results

Visualizing patterns of size-corrected labyrinthine shape variation in morphospace and in physical space permits characterization of high-level taxon-specific morphologies (Fig. 1): lorisoids, lemuroids, anthropoids, *Tarsius*, Adapiformes and Omomyiforms are well discriminated in PC1-PC2 space (32.05% of total shape variation), without almost any overlap. The labyrinth of *Pronycticebus* is closest in morphology to that of Adapinae and of Lemuroidea families such as Lepilemuridae, Lemuridae and Cheirogaleidae, and differs substantially from that of anthropoids (see Table 2). Anthropoid labyrinths show extension in the anteromedial to posterolateral direction, whereas the labyrinths of extant strepsirrhines and *Tarsius* tend to be compressed in this direction. The lateral canal of anthropoids is extended in the anteromedial to posterolateral direction while that of prosimians shows extension in the anterolateral to posteromedial direction (see Fig. 1-B, deformations along PC1). In *Pronycticebus*, Adapinae and Microchoerinae, the posterior semi-circular canal assumes a high position relative to the lateral canal (see Fig. 2 and Fig. 3), which results in partial fusion of the lateral and posterior semi-circular canals. Fossil specimens are well discriminated from extant strepsirrhines, anthropoids and *Tarsius* in PC1-PC2 space. Furthermore, the semi-circular canals of these Eocene primates are round, and their three semi-circular canals are of approximately similar size. This condition differs from that found in *Tarsius* and small bodied anthropoids: their anterior canal is relatively smaller (see also Fig. 1-B). The common crus of *Pronycticebus* is orthogonal to the plane of the lateral semi-circular canal, a condition that can also be observed in small-bodied Adapinae, like *Adapis*, and in some lemurs, such as *Cheirogaleus*, and in Lorisidae. The common crura of Microchoerine primates, of *Tarsius* and Anthroidea tend to point posteriorly (see Fig. 3).

Pronycticebus, *Adapis* and Lemuroidea exhibit similarities in cochlear shape, orientation and number of turns, measured following West 1985: their cochleae exhibit between 2 and 2.5 turns. In Lemuroidea, Lorisidae and Adapiformes, the turns of the cochlear spiral are in broad and close contact, which gives this structure a relatively more globose and flattened aspect. In contrast, the cochlear orientation and aspect of *Tarsius* and Microchoerinae resembles that of small anthropoids such as *Callithrix* (see Fig. 3): Microchoerinae, *Tarsius* and anthropoids exhibit cochleae oriented more anteriorly than those of Adapiformes and Lemuroidea (see Fig. 2 and

Fig. 3). Also, the second turn of their cochleae tends to stay further away from the plane of the first turn.

The phenetic similarity tree based on inner ear morphology is illustrated in Fig. 4. This tree gives indications about the affinities of taxon-specific labyrinthine shapes, and does not reflect the current view of primate phylogeny. This phenetic tree groups together extant platyrrhines and catarrhines, while Adapinea and *Pronycticebus* branch close to each other, and are distant from extant anthropoids. Microchoerinae and *Tarsius* branch together, but appear also distant from anthropoids..

Discussion

Our results show that inner ear morphology is a useful taxonomic marker, supporting the results of Lebrun et al. (2010). Our data show that the inner ear of *Pronycticebus* is morphologically closest to that of adapine Adapiformes, which indicates that inner ear morphological variation of Adapiformes is small. This result confirms that the inner ear of *Pronycticebus* can reasonably be used as a proxy for that of other putative Cercamoniinae primates like *Darwinius*.

Primate inner ear symplesiomorphies

The Eocene primates analysed in this study share similarities in the semi-circular canal system: their semi-circular canals are round and are of largely similar size, their posterior canal assumes a relatively high position, a consequence of which is its partial fusion with the lateral canal. We propose that these shared Adapiformes/Omomyiformes features represent symplesiomorphies of primate labyrinthine morphology.

Labyrinthine shape variation and cranial evolution

Our results suggest that, despite being a functionally constrained structure, a substantial residual part of primate labyrinthine morphology conveys non-functional information. This residual morphological variation may be related to specific cranial morphological characters. We observed in fossil Adapinae and Microchoerinae that the bony channels of the posterior limb of the lateral canal are merged with the inferior part of the posterior canal, forming a second common crus. The presence of a second common crus is found in a variety of extant and extinct placental and non

placental mammals (see for instance Benoit et al. 2012; Ekdale 2009; Hyrtl 1845; Schmelzle et al. 2007). In all extant specimens observed in this study, the posterior canal assumes a lower position relatively to the lateral canal, the consequence of which is the absence of fusion of the inferior part of the posterior canal with the posterior limb of the lateral canal. It may be asked how the presence of a second common crus in Eocene Adapinae and Microchoerinae and its absence in all extant primate specimens observed here relate to primate cranial evolution. Primates, and in particular anthropoids, exhibit a well documented general evolutionary trend towards increased encephalization during the Cenozoic (Jerison 1973, 1979; Radinski 1977), that is toward increasing their relative brain size. Evolving larger brain size implies modifications of the morphology of the braincase, and has a potential impact on the otic capsules and the surrounding petrous bone (Jeffery and Spoor 2004). The coronal orientation of the petrous bone has been shown to correlate with relative brain size in primates (Spoor 1997), which may influence the geometry of the labyrinth, and in particular the relative position of the semi-circular canals and the orientation of the cochlea. Also, in modern humans, the petrous bone is wedged between the cerebral temporal lobe and the cerebellum (see for instance Jeffery and Spoor 2004). This configuration is found in other extant primate species, such as *Otolemur garnetti*, *Tarsius syrichta* and *Callithrix jacchus* (see Fig. S2). In these species, the regions of the petrous bone holding the anterior and posterior canals are in close contact with the cerebral temporal lobes and the cerebellum. In *Adapis parisiensis*, the petrous bone being more laterally positioned relatively to the brain, the position and shape of the posterior and anterior canals are less likely to be influenced by brain structures (see Fig. S2). The lower position of the posterior canal relatively to the lateral canal in modern forms may be the result of a “packing” issue subsequent to the increasing volume of the brain during evolution. The orientation of the cochlea and the shape of the semi-circular canals may also covary with other aspects of cranial morphology, such as basicranial flexion. In order to better understand the non-functional component of primate labyrinthine morphological variation, a comprehensive covariation analysis between cranial and inner ear morphology is required.

Morphological differences between the two primate suborders

Researchers working on the dentitions of the earliest Omomyiforms and Adapiformes note only little difference (Gingerich 1986; Godinot 1978; Simons 1962; Szalay 1976). Hopefully, other cranial structures are useful to discriminate among primate groups. The middle ear region has long been studied (e.g., Gregory 1915, 1920; MacPhee and Cartmill 1986; Saban 1963), and differences in vascularisation and pneumatisation are found between both suborders. Our results suggest that the inner ear is another structure that differs in morphology between both suborders : despite the morphological similarities cited above, the inner ear of Eocene microchoerines on the one hand, and that of adapine Adapiformes and *Pronycticebus*, on the other, can be well distinguished, in particular in their cochlear and common crus orientation and in their cochlear aspect.

Tarsius and Omomyiformes on the one hand, and extant anthropoids on the other differ in overall labyrinthine shape (see Fig. 1 and Fig. 4). However, several inner ear characters link these extant and extinct haplorhines. Omomyiformes and *Tarsius* share similarities in the orientation of the common crus, shape of the canals (see Fig. 3). And even though Tarsiers have more spiral turns and have longer cochleae than Omomyids (Coleman and Boyer 2012), they share with small anthropoids some other aspects of morphology of the cochlea: we found that *Tarsius*, microchoerines and small anthropoids have anteriorly oriented cochleae exhibiting a second turn staying away from the plane of the first turn, and posteriorly oriented common crura. These three characters are candidate synapomorphies for the inner ears of haplorhines. On the other hand, extant and extinct strepsirrhine inner ears share morphological similarities. The inner ears of Adapinae and *Pronycticebus* are close in morphology to those of Malagasy lemurs. Lebrun et al. (2010) suggested that within extant strepsirrhines, the inner ear condition of Lemuroidea is primitive, while that of Lorisioidea is derived. Furthermore, Lebrun et al. 2010 found morphological affinities between the inner ears of Lemuroidea and Adapiformes and that of the dermopteran *Cynocephalus*, the three semi-circular canals of which are straight, round and approximately of similar size. However, as the inner ears of the dermopteran *Galeopterus* and of the scandantian *Tupaia* differ widely from those of primates, it cannot be ruled out that the similarities observed between *Cynocephalus* on the one hand, and Adapiformes and Lemuroidea on the other, represent morphological convergences. As such, it cannot be yet assessed

whether the labyrinthine similarities observed in Adapidae and Lemuroidea represent shared derived features within strepsirrhine primates rather than primate inner ear symplesiomorphies.

Is there evidence for a link between Adapiformes and Haplorhini?

There is virtually no similarity between the inner ears of Adapiformes and those of extant anthropoids, which gives no tangible arguments that would support the hypothesis of Franzen et al. (2009) that *Darwinius*, and other notharctid Adapiformes represent a group of primates which gave rise to anthropoids. Our results, on the other hand, do not contradict the classical hypothesis linking Adapiformes and toothcombed strepsirrhines, based on wrist and ankle synapomorphies (Beard et al. 1988).

The sample of fossil primates analyzed here does not allow to securely define synapomorphies of strepsirrhine inner ears. Such inferences would require the inclusion of other Adapiformes and earlier Omomyiformes. Also, extant anthropoids labyrinthine morphology may be well derived, as illustrated by the clear division of Adapiform-Omomyiform inner ear in PC1-PC2 space on the one hand, and of those of modern anthropoids on the other. Though shared characters exist between the inner ears of *Tarsius*, Omomyidae and small bodied anthropoids, further research is needed to assess whether they represent haplorhine synapomorphies.

Comparisons with inner ears of Eocene eosimiid (Beard et al. 1996; Jaeger et al. 1999) and to late Eocene African anthropoids (Seiffert et al. 2005), are thus required to understand the morphological evolution of this structure within haplorhines.

Conclusion

No synapomorphy was found between the labyrinths of *Pronycticebus* and those of modern anthropoids. On the contrary, *Pronycticebus* is closer in labyrinthine shape to extant strepsirrhines, which supports better the hypothesis that Cercamoniinae and other Adapiformes are the sister group of toothcombed primates. Also, candidate synapomorphies of haplorrhine inner ear have been proposed, which are absent in Adapiformes primates. Our results call for further

comparative analyses including the inner ear of early Eocene Adapiformes for which the cranium is preserved, such as *Cantius*, of early Eocene Omomyiformes such as *Teilhardina* and of fossil anthropoids.

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Figures and Tables

Fig. 1: Principal Components Analysis (PCA) of labyrinthine size-corrected shape variation. (a) Graphing the first two components of shape space, PC1 and PC2, shows differences in labyrinthine morphology across anthropoids, extant strepsirrhines, Eocene primates and *Tarsius*. Black symbols: strepsirrhines. Grey symbols: haplorhines. Triangles: Lorisoidea; Squares: Lemuroidea; Open circles: Adapinae; Filled circle: *Pronycticebus*; Stars: Platyrrhines; X: Catarrhines; Diamonds: *Tarsius*; +: Microchoerinae. Symbol size variation represents labyrinthine centroid size variation.

(b) Patterns of labyrinthine shape variation associated with PC1 and PC2, respectively. Grey arrows: anteromedial-to-posterolateral and anterolateral-to-posteromedial directions. T

Fig. 2: Left bony labyrinth of *Pronycticebus gaudryi*. The labyrinth is positioned in superior (a) and lateral (b) views (by convention, the lateral semicircular canal is positioned horizontally). Specimen: QU 11056. Scale bar: 5mm. Dashed arrows give the orientation of the common crus and of the cochlea. Note that the common crus is orthogonal to the plane of the lateral semi-circular canal.

Fig. 3: Left bony labyrinths of primates of (a) *Cheirogaleus major*, (b) *Galago moholi*, (c) *Adapis sp.*, (d) *Microchoerus erinaceus*, (e) *Tarsius spectrum*, (f) *Callithrix jacchus*. For each specimen, the labyrinth is positioned in superior (left) and lateral (right) views. Specimens: (a) MNHN MO 2002-87, (b) MNHN MO 1885-196, (c) MUNCH XV-1869-1530, (d) MONTA PR-1771, (e) AIM-ZU AS1821, (f) AIM-ZU 10168. Scale bar: 5 mm. Taxa of similar labyrinthine size to that of *Pronycticebus* were chosen. Dashed arrows give the orientation of the common crus and of the cochlea.

Fig. 4: Phenetic NJ tree based on inner ear morphology (average labyrinthine shape of taxa) reflecting bony labyrinth morphological affinities (size-corrected shape distances) between Adapinae, *Pronycticebus*, Lemuroidea, Lorisoidea, Microchoerinae, *Tarsius*, Platyrrhines, Catarrhines. Bootstrap values for 1000 resamplings are given at each node.

Table 1: List and protocol of data acquisition of the specimens used in the analyses.

Table 2: Procrustes and allometric corrected distance between the labyrinthine shape of *Pronycticebus* and that of extant and extinct primate family-specific mean labyrinthine shapes.

Figure S1: Landmarks used for geometric morphometric analysis of the bony labyrinth (specimen: *Lepilemur ruficaudatus* AIM-11054). Grey arrows: anteromedial-to-posterolateral and anterolateral-to-posteromedial directions.

Figure S2: Position within the skull of the left labyrinth of (a) *Adapis parisiensis*, (b) *Otolemur crassicaudatus*, (c) *Tarsius syrichta* and (d) *Callithrix jacchus*. Left: superior view of the skull and left labyrinth, the superior part of the calvaria being

virtually removed. Right : stereoscopic lateral view of the left labyrinth within the braincase. In *Adapis parisiensis*, the labyrinth is positioned in a more lateral position relatively to the brain structures. Arrows: in *Otolemur*, *Tarsius* and *Callithrix*, the posterior canal assumes a lower position relatively to the lateral canal.

Scale bars: 1cm. Specimens: (a) Cambridge M 538, (b) AIM-1841, (c) AIM-1732; (d) AIM-10168.

Literature Cited

- Beard KC, Dagosto M, Gebo DL, Godinot M (1988) Interrelationships among primate higher taxa. *Nature* 331:712-714
- Beard KC, Wang B, Dawson MR, Huang X, Tong Y (1996) Earliest complete dentition of an anthropoid primate from the late middle Eocene of Shanxi Province, China. *Science* 272:82–85
- Benoit J, Orliac M, Tabuce R (2012) The petrosal of *Chambius* (Macroscelidea, Afrotheria) from the Eocene of Djebel Chambi (Tunisia). *Journal of Systematic Paleontology* in press
- Coleman MN, Boyer DM (2012) Inner ear evolution in Primates through the Cenozoic. Implications for the evolution of hearing. *The Anatomical Record* 295:615-631
- Coleman MN, Colbert MW (2007) Technical Note: CT Thresholding Protocols for Taking Measurements on Three-Dimensional Models. *Am J Phys Anthropol* 133:723-725
- Coleman MN, Colbert MW (2010) Correlations between auditory structures and hearing sensitivity in non-human primates. *J Morph* 271:511-532
- Coleman MN, Kay RF, Colbert MW (2010) Auditory morphology and hearing sensitivity in fossil New World monkeys. *The Anatomical Record* 293:1711-1721
- Couette S, Lebrun R, Godinot M (2011) The haplorhine/strepsirhine position of *Darwinius masillae*: New insights based on the CT analysis of *Pronycticebus gaudryi* middle ear morphology. Paper presented at the 22nd International Senckenberg Conference. The World at the Time of Messel: Puzzles in Palaeobiology, Palaeoenvironment and the History of Early Primates, Frankfurt, 15-19th November 2011
- Echteler SM, Fay RR, Popper AN (1994) Structure of the mammalian cochlea. In: Fay RR, Popper AN (eds) *Comparative Hearing: Mammals*. Springer-Verlag, New York, pp 134-171
- Ekdale EG (2009) Variation within the bony labyrinth of mammals. University of Texas, PhD dissertation, Austin
- Felsenstein J (1989) PHYLIP - Phylogeny Inference Package (Version 3.2). *Cladistics* 5:164-166
- Franzen JL (1994) The Messel Primates and Anthropoid Origins. In: Fleagle JG, Kay RF (eds) *Anthropoid Origins*. pp 99-122
- Franzen JL, Gingerich PD, Habersetzer J, Hurum JH, von Koenigswald W, Smith BH (2009) Complete primate skeleton from the Middle Eocene of Messel in Germany: morphology and paleobiology. *PLoS ONE* 4 (5):e5723
- Gingerich PD (1973) Anatomy of the temporal bone in the Oligocene anthropoid *Apidium* and the origin of Anthroipoidea. *Folia Primatol* 19 (5):329-337
- Gingerich PD (1975) A new genus of Adapidae (Mammalia, Primates) from the late Eocene of southern France, and its significance for the origin of higher primates. *Contributions from the Museum of Paleontology, University of Michigan* 24:163-170
- Gingerich PD (1981) Eocene Adapidae, paleobiogeography, and the origin of South American Platyrrhini. In: Ciochon RL, Chiarelli AB (eds) *Evolutionary Biology of the New World Monkeys and Continental Drift*. Plenum, New York, pp 123-138
- Gingerich PD (1986) Early Eocene *Cantius torresi*— oldest primate of modern aspect from North America. *Nature* 320: 319–321. *Nature* 320:319-321
- Gingerich PD, Franzen JL, Habersetzer J, Hurum JH, Smith BH (2010) *Darwinius masillae* is a Haplorhine - Reply to Williams et al. (2010). *J Hum Evol* 59 (5):574-579
- Gingerich PD, Schoeninger M (1977) The fossil record and primate phylogeny. *J Hum Evol* 6:483-505

- Gleich O, Dooling RJ, Manley GA (2005) Audiogram, body mass, and basilar papilla length: correlations in birds and predictions for extinct archosaurs. *Naturwissenschaften* 92:595-598
- Godinot M (1978) Un nouvel Adapidé (Primate) de l'Eocène inférieur de Provence. *Comptes rendus de l'Académie des Sciences de Paris, Série D* 286:1869-1872
- Godinot M (1998) A Summary of Adapiform Systematics and Phylogeny. *Folia Primatol* 69 (suppl 1):218-249
- Grandidier G (1904) Un nouveau lémurien fossile de France, le *Pronycticebus gaudryi*. *Bulletins du Muséum national d'histoire naturelle, Paris* 10:9-13
- Gregory WK (1915) I: On the relationship of the Eocene Lemur *Notharctus* to the adapidae and the other Primates. II: On the classification and phylogeny of the Lemuroidea. *Bulletin of the Geological Society of America* 26:419-446
- Gregory WK (1920) On the structure and relations of *Notharctus*, an American Eocene primate. *Bulletins of the American Museum of Natural History* 42:95-263
- Gunz P, Ramsier M, Kuhrig M, Hublin J-J, Spoor F (2012) The mammalian bony labyrinth reconsidered, introducing a comprehensive geometric morphometric approach. *J Anat* 6:529-543
- Herbomel E, Godinot M (2011) A new species of *Agerinia* (Primates, Adapiformes) and its bearing on the phylogenetic affinities of *Darwinius masillae*. Paper presented at the 22nd International Senckenberg Conference. The World at the Time of Messel: Puzzles in Palaeobiology, Palaeoenvironment and the History of Early Primates, Frankfurt, 15-19th November 2011
- Hurum JH (2011) Cranial morphology of the Eocene primate *Darwinius masillae*. Paper presented at the 22nd International Senckenberg Conference. The World at the Time of Messel: Puzzles in Palaeobiology, Palaeoenvironment, and the History of early Primates, Frankfurt,
- Hyrtil J (1845) Vergleichend-anatomische Untersuchungen über das innere Gehörorgan des Menschen und der Säugethiere. Friedrich Ehrlich, Prague
- Jaeger J-J, Thein T, Benammi M, Chaimanee Y, Soe AN, Thit L, Than T, San W, Ducrocq S (1999) A new primate from the middle Eocene of Myanmar and Asian early origin of Anthropoids. *Science* 286:528-530
- Jeffery N, Spoor F (2004) Prenatal growth and development of the modern human labyrinth. *J Anat* 204:71-92
- Jerison HJ (1973) *Evolution of the Brain and Intelligence*. Academic Press, New York
- Jerison HJ (1979) Brain, Body and Encephalization in Early Primates. *J Hum Evol* 8:615-635
- Kay RF, Ross C, Williams BA (1997) Anthropoid Origin. *Science* 275:797-803
- Kirk EC, Gosselin-Ildari AD (2009) Cochlear labyrinth volume and hearing abilities in primates. *The Anatomical Record* 292:765-776
- Le Gros Clark WF (1934) On the skull structure of *Pronycticebus gaudryi*. *Proc Zool Soc Lond* (1):19-27
- Lebrun R (2008) Evolution and Development of the Strepsirrhine Primate Skull. Ph.D. Thesis in Paleontology, Université Montpellier II, University Zürich Irchel,
- Lebrun R, Couette S, Godinot M (2011) The labyrinthine morphology of *Pronycticebus gaudryi* (Primates, Adapiformes). Paper presented at the 22nd International Senckenberg Conference. The World at the Time of Messel: Puzzles in Palaeobiology, Palaeoenvironment and the History of Early Primates, Frankfurt, 15-19th November 2011
- Lebrun R, Ponce de León MS, Tafforeau P, Zollikofer CPE (2010) Deep evolutionary roots of strepsirrhine primate labyrinthine morphology. *J Anat* 216:368-380

- Lockwood C, Kimbel WH, Lynch JM (2004) Morphometrics and hominoid phylogeny: Support for a chimpanzee–human clade and differentiation among great ape subspecies. *P Natl Acad Sci USA* 101:4356-4360
- MacPhee RDE, Cartmill M (1986) Basicranial Structures and Primate Systematics. In: Swindler DR (ed) *Comparative Primate Biology. Vol. I. Systematics, Evolution, and Anatomy*. Alan R. Liss, New York, pp 219-275
- Marivaux L, Antoine P-O, Baqui SRH, Benammi M, Chaimanee Y, Crochet J-Y, de Franceschi D, Iqbal N, Jaeger J-J, Metais G, Roohi G, Welcomme J-L (2005) Anthropoid primates from the Oligocene of Pakistan (Bugti Hills): data on early anthropoid evolution and biogeography. *P Natl Acad Sci USA* 102:8436-8441
- Ni X, Wang Y, Hu Y, Li C (2004) A euprimate skull from the early Eocene of China. *Nature* 427:65-68
- Radinski LB (1977) Early primate brains: facts and fiction. *J Hum Evol* 6:79-86
- Rasmussen DT (1986) Anthropoid origins: a possible solution to the Adapidae-Omomyidae paradox. *J Hum Evol* 15:1-12
- Rasmussen DT (1990) The phylogenetic position of *Mahgarita stevensi*: Protoanthropoid or lemuroid? *Int J Primatol* 11:439-469
- Ross CF, Williams BA, Kay RF (1998) Phylogenetic analysis of anthropoid relationships. *J Hum Evol* 35:221-306
- Saban R (1963) Contribution a l'étude de l'os temporal des primates. Description chez l'homme et les prosimiens. Anatomie comparée et phylogénie. Mémoires du Muséum National d'Histoire Naturelle de Paris, série A 29:1-378
- Schmelzle T, Sánchez-Villagra MR, Maier W (2007) Vestibular labyrinth diversity in diprotodontian marsupial mammals. *Mamm Stud* 32:83-97
- Seiffert ER, Simons CVM, Clyde WC, Rossie JB, Attia Y, Bown TM, Chatrath PS, Mathison ME (2005) Basal anthropoids from Egypt and the antiquity of Africa's higher primate radiation. *Science* 310:300-304
- Silcox MT, Bloch JJ, Boyer DM, Godinot M, Ryan TM, Spoor F, Walker A (2009) The semicircular canal system in early primates and euprimates. *J Hum Evol* 56:315-327
- Simons EL (1962) A new Eocene primate genus, *Cantius*, and a revision of some allied European lemuroids. *Bulletin of the British Museum (Natural History), Geology* 7:1-36
- Specht M (2007) Spherical Surface Parameterization and its Application to Geometric Morphometric Analysis of the Braincase. Ph.D. Dissertation, University of Zürich Irchel, Zürich
- Specht M, Lebrun R, Zollikofer CPE (2007) Visualizing Shape Transformation between Chimpanzee and Human Braincases. *Visual Comput* 23 (9-11):743-751
- Spoor C, Zonneveld F (1998) Comparative review of the human bony labyrinth. *Am J Phys Anthropol Suppl* 27:211-251
- Spoor F (1997) Spoor F (1997) Basicranial architecture and relative brain size of Sts 5. (*Australopithecus africanus*) and other Plio-Pleistocene hominids. *South African J Sci* 93:182-187
- Spoor F, Garland TJR, Krovitz G, Ryan TM, Silcox MT, Walker A (2007) The primate semicircular canal system and locomotion. *P Natl Acad Sci USA* 104 (26):10808-10812
- Spoor F, Zonneveld F, Macho G (1993) Linear measurements of cortical bone and dental enamel by computed tomography: Applications and problems. *Am J Phys Anthropol* 91 (4):469-484
- Szalay FS (1971) The European adapid primates *Agerina* and *Pronycticebus*. *American Museum novitates* 2466:1-18

- Szalay FS (1976) Systematics of the Omomyidae (Tarsiiformes, Primates). Taxonomy, Phylogeny, and Adaptations. B Am Mus Nat Hist 156:157-450
- Tafforeau P, Boistel R, Boller E, Bravin A, Brunet M, Chaimanee Y, Cloetens P, Feist M, Hoszowska J, Jaeger J-J, Kay RF, Lazzari V, Marivaux L, Nel A, Nemoz C, Thibault X, Vignaud P, Zabler S (2006) Applications of X-ray synchrotron microtomography for non-destructive 3D studies of paleontological specimens. Appl Phys A-Mater 83 (2):195-202
- Walker A, Ryan TM, Silcox MT, Simons EL, Spoor F (2008) The semicircular canal system and locomotion: the case of extinct lemuroids and loroids. Evol Anthropol 17:135-145
- West CD (1985) The relationship of the spiral turns of the cochlea and the length of the basilar membrane to the range of audible frequencies in ground dwelling mammals. J Acoust Soc Am 77 (3):1091-1100
- Williams BA, Kay RF, Kirk EC, Ross CF (2010) *Darwinius masillae* is a strepsirrhine - a reply to Franzen et al. (2009). J Hum Evol 59 (5):574-579